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Hurricane Andrew and a Florida Fig Pollination Mutualism: Resilience of an Obligate Interaction[1]

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ABSTRACT

The obligate mutualism between figs and their species-specific pollinator wasps has been thought to be relatively fragile in the face of population fluctuations of either mutualist. Here we report on the recovery of a Florida fig pollination mutualism devastated by Hurricane Andrew in August 1992. Damage to *Ficus aurea* included loss of all leaves and fruits and many branches, as well as the presumed local extinction of its pollinator *Pegoscapus jimenezi*. Within five months, however, fig flowering plenology and fig wasp abundance (measured by the number of pollinators entering inflorescences) had recovered to near prehurricane levels. Unusual phenological traits of *F. aurea* may have aided in the rapid reestablishment of pollinator populations; in addition, the wasps may have previously underappreciated capacities for long distance movements. This study suggests that obligate interactions can be surprisingly resilient to certain population-level catastrophes.

Key words: *Agaoninae; climate;* Ficus aurea; *figs; Florida; Hurricane Andrew; insects; mutualism; pollination; population dynamics.*

THE INTERACTION BETWEEN MONOECIOUS FIGS (*Ficus* spp.) and their species-specific, obligate pollinator wasps (Chalcidoidea: Agaoninae) is one of the best-known plant/animal mutualisms, and one that has become emblematic of the tropics. Fig wasps pollinate fig flowers, then lay eggs in some of them; wasp offspring feed on developing seeds. The pollen-carrying adult females live a few days at most and are believed to have poor flight abilities. A wasp departing from one fig must therefore find another fig in the correct developmental phase that is quite close in both space and time if she is to successfully transport pollen and to reproduce. For most fig species, trees within a population flower out of synchrony with each other and year-round, thereby increasing the likelihood that wasps will be able to transfer pollen successfully between trees. The natural history of this interaction might appear to restrict it to relatively stable aseasonal habitats, since climatic conditions that either reduced survivorship of the searching wasps, caused abortion of developing figs, or created a temporal gap in the flowering sequence could lead to the local extinction of the pollinator population. In this case, figs would fail to reproduce successfully until the correct wasp species was able to colonize from an unaffected refuge.

In light of the apparent fragility of this interaction, it is interesting to note that although figs and fig wasps are most abundant and most thoroughly studied in the equatorial tropics, they occupy a very broad latitudinal range (45°N–35°S) (Corner 1958, Berg 1989, Bronstein 1989). Both mutualists clearly persist year-round in certain seasonal, subtropical locations, including Hong Kong (Hill 1967, Corlett 1984, Corlett *et al.* 1990), South Africa (Baijnath & Ramcharun 1983, 1988; Compton 1993), south Florida, USA (Bronstein 1989; Bronstein & Patel 1992a, b) and Sonora, Mexico (Smith 1994). In Florida and Mexico, pollinator populations do become greatly reduced during certain winters, but trees flower continuously and pollinator numbers rebound by late spring (Smith 1994, J. Bronstein & M. Hossaert-McKey, unpublished data). These observations suggest a resilience to the fig/pollinator interaction that has not been expected from its unusual natural history.

A unique natural experiment allowing us to examine the resilience of a fig/pollinator mutualism directly took place in August, 1992 when Hurricane Andrew, one of the most intense hurricanes of this

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TABLE 1. *Developmental stages of fig inflorescences. Modified from Galil and Eisikowitch 1968; see also Verkerke 1989.*

A phase (pre-female)	Immature flowers present. *F. aurea* inflorescences may stay in this phase from 2 d to over 9 mo (Bronstein & Patel 1992a).
B phase (female)	Female flowers become receptive to pollination, volatile attractant is released, female agaonine wasps enter the inflorescence and then pollinate and oviposit. This phase lasts from 1 d to 3 wk in *F. aurea.*
C phase (interfloral)	Fig seeds and fig wasp larvae develop within the ovaries. This phase is temperature-dependent in *F. aurea,* lasting 4–7 wk (Bronstein & Patel 1992b).
D phase (male)	Anthers mature, agaonine wasps emerge within the fig and mate there, females actively load pollen while males bore an exit passage through the fig wall, and females then depart. This phase lasts 1–2 d.
E phase (post-floral)	Figs ripen and either are dispersed or fall from the tree. This phase lasts 1–5 d in *F. aurea.*

century, passed through south Florida, USA. Since 1988, we have been studying the Florida strangling fig, *Ficus aurea*, its pollinator *Pegoscapus jimenezi*, and a large community of specialized nonpollinating wasp species near Miami. At our study site, the hurricane destroyed all leaves and developing figs, many tree limbs, and possibly every wasp associated with *Ficus aurea*. We describe the recovery of these species during the subsequent sixteen months. Specifically, we address the following questions. What was the immediate effect of the hurricane on the *Ficus aurea–Pegoscapus jimenezi* mutualism? Did pollinators subsequently reestablish at the study site? If so, how do their numbers compare to prehurricane levels? Have fig phenological patterns documented prior to the hurricane become reestablished since then?

MATERIALS AND METHODS

STUDY SYSTEM.—The mutualism between the 350 monoecious fig species and their obligate, species-specific pollinators can be summarized as follows (see also Janzen 1979, Berg & Wiebes 1992, Bronstein 1992). Pollen-carrying female agaonine wasps arrive at fig trees when they are in flower. Inflorescences (referred to here as figs) are hollow multiple receptacles lined with hundreds of male and female florets. At the time wasps arrive, only the female florets are receptive (female or B phase; see Table 1 for a summary of fig developmental phases). The wasps enter the fig via a bract-covered pore, usually becoming trapped in the process. Once inside, they deposit pollen on the stigmas, then oviposit via the styles into some of the ovaries. Seed-eating wasp larvae and some intact seeds mature over the next several weeks (interfloral or C phase). When the wasps reach adulthood, they copulate within the fig. Females then collect pollen from the newly mature anthers, while males tunnel back through the wall of the fig. The inseminated females then depart with pollen (male or D phase) in search of a female-phase fig. At most times of year in most species, figs on a given tree are developmentally synchronized, forcing the searching female wasps to depart their natal tree. Free-living adults can survive a few days at most (Kjellberg *et al.* 1988); they do not feed, and mortality in flight is probably 95–99 percent (Bronstein 1989, Herre 1989).

Ficus aurea Nuttall is a Caribbean Basin species that reaches its northern limit in south central Florida; it is one of two fig species native to the United States (Condit 1969). In south Florida it grows abundantly on hammocks (hardwood stands surrounded by lower, wetter vegetation) and keys, as well as along watercourses. Trees are large, reaching a height of 15 m and a spread of 25 m or more, and often show an epiphytic, strangling habit (Condit 1969). The inflorescences are subglobose and vary both in size (7–12 mm diameter) and color at maturity. *Ficus aurea* is pollinated exclusively by the agaonine wasp *Pegoscapus jimenezi* (Grandi) (Wiebes 1983). The biology of this wasp and its interactions with *F. aurea* have been documented by Frank (1983, 1984), Bronstein (1989), and Bronstein and Patel (1992a, b). At least twenty other arthropod species, including host-specific competitors, predators, and commensal species, also mature within *F. aurea* figs (Nadel *et al.* 1992); the biology of these species is still poorly known.

The study population consists of about 50 *F. aurea* trees on the University of Miami campus in Coral Gables, Florida (25°43′N, 80°16′W). These individuals range in size from 40 to 350 cm dbh and are found in hammock remnants along old canals, with the majority in areas removed from human disturbance. There is no evidence that these trees were planted; *F. aurea* rapidly and naturally recruits along canals in south Florida. We have identified no consistent differences between the University population and *F. aurea* trees in less disturbed sites in south Florida (Frank 1983, unpublished data, Bancroft & Bowman 1989, D. McKey, M. Hossaert-McKey, & J. Bronstein, unpublished data).

FIG PHENOLOGICAL PATTERNS.—Phenologies of 31 *F. aurea* trees were documented every 1–3 weeks from February 1991 until the week of the hurricane (24 August 1992). Due to our absence from the study site, no censuses were conducted for the four subsequent months, with the exception of 25 August and 15 September. Censuses resumed at the 1–3 week frequency in January 1993 and continued through December 1993. At each census we thoroughly scanned each tree, noting whether it bore developing figs and, if so, the number of developmental phases present (from 0 to 5; see Table 1). Observations were made on 34 census dates in 1991, 22 census dates in 1992, and 19 census dates in 1993, for a total of 2062 tree-dates.

Methods of analysis were designed to take into account several unusual features of *F. aurea* flowering phenology (see Bronstein & Patel 1992a, b). Like other fig species, *F. aurea* populations flower year-round. In contrast to other species, however, *F. aurea* trees commonly bear figs in a diversity of developmental phases year-round; in most other fig species, individual trees bear synchronized crops one or more times each year, separated by prolonged nonreproductive periods. *Ficus aurea* phenological patterns are strongly seasonal, however. During certain seasons all figs on a given tree are in the same phase; in particular, it is common for a tree to bear only pre-female (A-phase) figs, which can remain dormant for months before resuming growth and becoming attractive to pollinators. At other times of year, a greater diversity of developmental phases is present (Bronstein & Patel 1992a, J. Bronstein, unpublished data).

In order to specifically identify phenological changes that may have been related to the hurricane rather than to these predictable seasonal effects, we compared tree-level phenologies across years, then within seasons across years. Seasons were defined as follows, based on long-term temperature and precipitation data (see Bronstein & Patel 1992a): spring (March–May), summer (June–September), autumn (October–November), and winter (December–February; winter 1991, for example, extended from December 1991–February 1992). For each season and year, we calculated two phenological indices. The first was the proportion of census dates on which at least some figs were developing on the average tree. We predicted that if the hurricane led to flowering failure, then this index of flowering frequency would have been significantly lower in the posthurricane year or seasons than in matched prehurricane years or seasons. The second index was the number of developmental phases present on the average tree. If the hurricane led to within-tree synchronization of fig development, then this synchrony index should have been significantly lower in the posthurricane year or seasons than in matched prehurricane years or seasons. Analyses of variance were used in each case to compare each index across years or seasons, followed by post-hoc Scheffé tests to test specific hypotheses about whether the hurricane may have been responsible for any significant effect. Data on proportions of trees in flower were arcsine transformed prior to statistical analysis.

FIG WASP PRESENCE AND ABUNDANCE.—Agaonine wasps usually become trapped and die within the figs they enter, providing a useful tool for assessing spatial and temporal patterns for their presence and abundance within a given population. At each census of each tree, whenever female-phase figs were present, a sample of 20–30 was randomly collected. At a later date, a subsample (usually 10) was dissected under the stereomicroscope and all trapped pollinators were counted. A total of 2405 figs from 34 trees were examined from 30 census dates in 1991, 17 census dates in 1992, and 14 census dates in 1993.

Censuses since 1988 have revealed consistent seasonal variation in the mean number of pollinators trapped per fig: numbers are elevated in late spring and depressed in winter and summer (J. Bronstein & M. Hossaert-McKey, unpublished data). As in our phenological analyses, in order to identify patterns of wasp abundance that may have been specifically related to the hurricane, we drew comparisons across years and within seasons. If Hurricane Andrew strongly depressed or eliminated local pollinator populations, then for a given year or season, the average number of trapped pollinators per fig should have been significantly lower in the posthurricane samples than in prehurricane samples. Statistical analyses were similar to those described above for phenological data.

RESULTS

IMMEDIATE EFFECTS OF THE HURRICANE.—In the early morning hours of 24 August, 1992, Hurricane Andrew made landfall near Homestead, Florida, about 30 km south of the study site. The storm surges and violent winds, with gusts exceeding 300 kph, were characteristic of a Category 4 hurricane on the Saffir/Simpson scale; barometric pressure at landfall (922 mb) was the third lowest recorded in this century for a United States hurricane (Rappaport & Sheets 1993). Maximum sustained wind speeds near our study site are currently estimated to have been about 170 kph (Dorschner 1993). While intense, Hurricane Andrew was relatively compact, with maximum winds in the eyewall extending to a radius of about 20 km (Federal Emergency Management Agency 1993). It caused extensive damage to property and to both agricultural and natural ecosystems (Odgen 1992, Campbell *et al.* 1993, Rappaport & Sheets 1993, Loope *et al.* 1994, Pimm *et al.* 1994, Smith *et al.* 1994).

Despite the extreme winds, no *F. aurea* tree at our study site snapped or was uprooted in the hurricane; none was killed by the hurricane, and none has died subsequently. Every tree, however, lost limbs and branches. Three weeks after the hurricane (15 September), six of the 31 census trees (19%) were noted to have suffered minor damage (*i.e.,* few snapped branches), 13 (42%) moderate damage (some loss of major branches), and 12 (39%) major damage (loss of many major branches and/or damage to the trunk). The lost branches were often the most easily censused ones (those within 1–2 m of the ground). We were subsequently forced to stop censusing four trees on which it had become impossible to closely observe fruiting branches.

The hurricane occurred during a typically active reproductive season for *F. aurea*. At the final prehurricane census (18 August), every tree bore at least some developing figs in an average of 2.2 of the five developmental phases listed in Table 1 (compared to 98% of trees reproductive and 2.2 phases present for the average tree at the average census over the entire study). Intensive observations on the day after the hurricane revealed that no census tree had retained either any figs or any leaves. During the next three weeks, however, most trees began flushing new leaves and some initiated new (A-phase) figs. When regular censuses resumed on 11 January 1993, 96.5 percent of the trees (30 of 31) bore both leaves and figs.

Pollinator abundance had been high prior to the hurricane. An average of 3.6 female wasps was trapped in 10 newly pollinated figs sampled from the one tree that was in female phase during the last prehurricane census (18 August), compared to a study-long average of 2.2 per fig. On that date, 20 trees (64%) bore figs in C phase (*i.e.,* had wasp larvae developing within them), while seven trees (23%) bore D-phase figs and thus were in the process of releasing mature wasps. Since no figs had been noted on census trees immediately after the hurricane, it seems probable that all or nearly all wasp larvae were lost at this location. The minute (1–2 mm) free-living adult wasps presumably perished in the high winds or rain, or else were blown far from the study site.

LONGER-TERM EFFECTS ON FIG PHENOLOGY.—Under normal conditions, *F. aurea* trees almost always bear figs in some developmental stage. The average tree bore figs on 99.5 percent of the 1991 census dates and 98.2 percent of the prehurricane 1992 census dates. The average in 1993 was only slightly lower, 97.1 percent of all census dates (Fig. 1). The difference in flowering frequency across years was highly significant (ANOVA: $F = 4.695$; df = 2, 71; $P = 0.005$), although post-hoc comparisons indicate that the only pair of years that differed significantly were 1991 and 1993 (Scheffé test, $P = 0.009$). More specifically, flowering was significantly more frequent in autumn 1991 than in autumn 1993, and more frequent in the prehurricane winter of 1991 than in either of the posthurricane winters, 1992 and 1993 (Fig. 1).

Within-tree synchrony, measured as the average number of fig developmental phases present, also varied significantly across census years (ANOVA: $F = 4.233$; df = 2, 71; $P = 0.008$). The only pair of years that differed significantly from each other were 1991 and 1992 (Scheffé test, $P = 0.013$). The posthurricane year of 1993 showed an intermediate level of within-tree synchrony. The only significant differences at the seasonal level were between the prehurricane winter of 1991 and the two posthurricane winters, 1992 and 1993: within-tree phenologies were relatively synchronized in the posthurricane winters (Fig. 2).

In the context of our specific hypotheses, the only possible phenological effect of Hurricane Andrew that we could identify was that relatively fewer trees flowered, and those trees that did flower showed increased levels of within-tree synchrony, during the two posthurricane winters relative to the one prehurricane winter. However, there are two reasons to doubt whether these patterns were in fact hurricane-related. First, these effects were restricted to winter; the rest of the posthurricane year resembled the two prehurricane years. Second, phenological patterns documented during the posthurricane winters of 1992 and 1993 generally resemble patterns

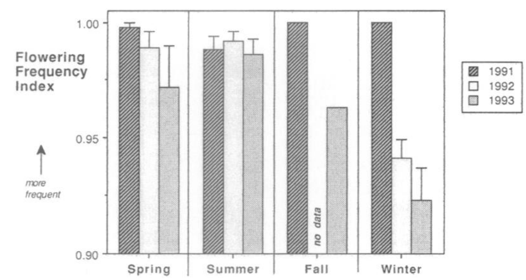

FIGURE 1. Seasonal patterns in flowering frequency, measured as the average proportion ($\pm$ 1 SE) of all census dates in a given season on which individual *F. aurea* trees bore at least some developing figs. For definitions of seasons, see text. The only within-season comparisons that were significant were the following: flowering in autumn 1991 was more frequent than in autumn 1993 (Scheffé test, $P < 0.0001$), and flowering in winter 1991 was more frequent than in either winter 1992 or winter 1993 ($P < 0.0001$).

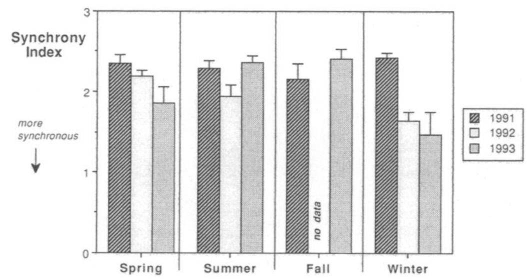

FIGURE 2. Seasonal patterns in within-tree phenological asynchrony, measured as the average number of fig developmental stages ($\pm$ 1 SE) present on individual trees in a given season. Seasons are defined in the text and developmental stages are defined in Table 1. The only within-season comparisons that were significant were the following: trees showed greater within-tree asynchrony in winter 1991 than in either winter 1992 (Scheffé test, $P = 0.002$) or winter 1993 ($P = 0.003$).

from the winters of 1988 and 1989, documented elsewhere (Bronstein & Patel 1992a). During this six-year study, the winter of 1991 has stood out as a time of exceptionally high reproductive activity for *F. aurea*.

LONGER-TERM EFFECTS ON WASP ABUNDANCE.—Numbers of pollinators trapped per fig were statistically identical in samples taken before the hurricane and those collected 5–16 months after it. Interyear differences in average wasp numbers per fig were not significant (ANOVA: $F = 0.167$; df = 2, 58; $P = 0.846$). Seasonal comparisons indicated that average wasp numbers per fig tended to be higher in prehurricane years in spring and autumn, and higher in posthurricane samples in summer (Fig. 3), but these differences were not statistically significant. Furthermore, samples collected in January–February 1993, 5 to 6 months after the hurricane, had nearly identical numbers of pollinators per fig as they had during the same period the previous year (Fig. 3; Scheffé test, $P = 0.8774$).

DISCUSSION

HURRICANE IMPACTS ON TREES AND INSECTS.—*Ficus aurea* trees apparently suffered little lasting damage from Hurricane Andrew. Like other Caribbean tree species studied in the aftermath of hurricanes (Brokaw & Walker 1991), including Hurricane Andrew (Loope *et al.* 1994), defoliation was the most common form of damage, followed by the loss of branches. New *F. aurea* leaves were reappearing within 3 weeks and leafing recovery was completed within 5 months, again consistent with recent posthurricane observations of native Caribbean trees (Brokaw & Walker 1991, Walker 1991, Yih *et al.* 1991, You & Petty 1991, Wunderle *et al.* 1992, Looper *et al.* 1994).

While posthurricane recovery of tree species has been relatively well-studied, consequences for their interactions with insects remain largely speculative. Little is known about how insects respond to climatic events as severe and unpredictable as hurricanes. In the short term, mortality can be extremely high, particularly for insects that do not occupy sheltered refuges (Wolcott 1941, Waide 1991, Willig & Camilo 1991, Loope *et al.* 1994). Longer-term recovery may depend on how rapidly their food supply recovers. For herbivorous insects able

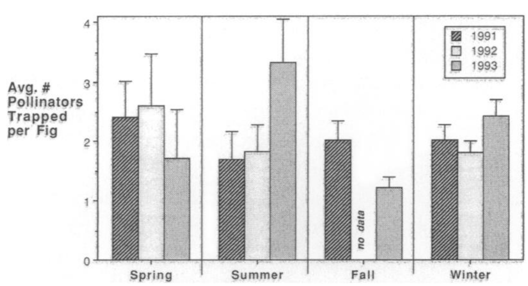

FIGURE 3. Seasonal patterns in wasp abundance, measured as the average number of pollinator wasps ($\pm$ 1 SE) entering female-phase figs in a given season. For definitions of seasons, see text. None of the within-season differences was statistically significant.

to survive a hurricane itself, the period of leaf absence that follows may prove fatal. However, the subsequent, synchronous leaf flush can lead to explosive growth of herbivore populations (Waide 1991, but see Willig & Camilo 1991) and to even higher impacts of herbivory on host plants (Wolcott 1932, Torres 1992). Insects that feed on flowers and fruits face similar short-term problems, since these resources are often eliminated during hurricanes. Some of these insects are likely to be pollinators and seed dispersers, which exploit flowers and fruits mutualistically. Decreased mutualist populations can be expected to have deleterious consequences for plant reproductive success, effects that may linger for some time. These consequences should be particularly pronounced when the mutualist is obligate and species-specific, as in fig/fig wasp interaction.

Recovery of a fig pollination mutualism.—There are good reasons to expect slow recoveries of figs and their pollinators from extreme climatic events. Fig wasp larvae mature, pupate, and mate exclusively within the inflorescences of a single fig species; any event that causes loss of inflorescences will therefore kill them. The free-living adults survive no longer than 1–3 days in the wild, and are so small (1–2 mm) that they are presumed to have minimal abilities to actively search for their obligate host plants or to survive harsh climatic conditions (Kjellberg *et al.* 1988). Considerable flowering asynchrony among trees in most fig populations increases the change that fig wasps will be able to locate a suitable tree within a few hours or days. Figs rarely grow where seasonality is severe enough to force gaps in flowering, and when they are planted in such sites, pollinator populations do not establish (Bronstein 1989). Hence, we expected that hurricane-related flowering failure would cause catastrophic mortality of fig wasps, and, in turn, massive reproductive failure in figs.

Confounding these expectations, the *Ficus aurea–Pegoscapus jimenezi* interaction at our study site has shown remarkably rapid recovery from Hurricane Andrew, one of the most severe hurricanes of the century. As far as we were able to judge from careful observations, every developing fig was stripped from our census trees and fig wasps in every developmental stage were presumably killed. Therefore, when the first posthurricane fig crops reached female phase (probably in late September or early October 1992), the only wasps that could have pollinated them would have been ones that had either survived in the refuge of the few retained figs that we may have overlooked, or ones that had migrated in from less affected areas. (It is possible that some wasps matured and emerged successfully from figs that were blown from the trees. However, fallen figs rot within a few days, and the next crop of receptive figs was not yet present three weeks after the hurricane. We therefore do not consider fallen figs to have been a possible source of posthurricane colonizing wasps.) By mid-January 1993, less than 5 months after the hurricane, wasp populations were large enough that the average number of pollinators entering receptive figs was indistinguishable from the previous year. Furthermore, the large community of nonpollinator wasp species, several of which are specific to *F. aurea*, had reestablished in a diversity and abundance roughly comparable to prehurricane levels (J.-Y. Rasplus, M. Hossaert-McKey, & J. Bronstein, unpublished data). Since wasp development takes about 43 days during autumn and winter (Bronstein & Patel 1992b), this recovery had taken less than four wasp generations.

It should be noted that we assessed fig wasp abundance on the basis of the numbers trapped within receptive, female-phase figs. Since many trees lost branches that might otherwise have borne figs, it is possible that *absolute* wasp numbers have in fact been lower since the hurricane. Since we did not attempt to measure the total number of figs on trees at one time (usually in the tens or hundreds of thousands), nor the growth of new branches, we cannot quantify such changes in wasp population sizes. Our data strongly imply, however, that the prehurricane ratio of pollinators to female-phase *F. aurea* inflorescences was rapidly reestablished after the hurricane.

How could recovery have proceeded so rapidly? We believe that two interacting phenomena may have been responsible. These are:

(1) *Fig wasps may have longer than expected travel distances.* Fig wasps locate their hosts by using species-specific volatile attractants released by female-phase inflorescences (Ware *et al.* 1993; Hossaert-McKey *et al.* 1994). Current knowledge of maximum travel distances of fig wasps is based on anecdotes: fig trees isolated by tens or even hundreds of kilometers from their nearest neighbors have occasionally been known to attract pollinators (Pemberton 1934, Ramirez 1970, Compton *et al.* 1988, Ware & Compton 1992). It is unknown, however, how common such events might be; they presumably result when the wasps are blown considerable distances into areas in which they can then navigate

using fig volatiles. Ongoing studies documenting exceptionally high levels of heterozygosity of neotropical figs (including *F. aurea* at our study site; J. Nason, unpublished data) are suggesting that such events may be far more common that previously believed (Hamrick & Murawski 1991, J. Nason & E. A. Herre, unpublished data). In the present case, we suspect that the most important source of immigrants may have been the large *F. aurea* population in Everglades National Park, about 60 km south of the study site, located well outside the eyewall of Hurricane Andrew. Many of the Everglades hardwood hammocks in which *F. aurea* is abundant (pers. obs.) suffered relatively little hurricane damage (Loope *et al.* 1994).

(2) *Rapid reestablishment of asynchronous fig phenologies may speed the recovery of pollinator populations.* Most monoecious fig species exhibit within-tree flowering synchrony but population-level asynchrony (Bronstein 1989). Simulation models indicate that catastrophic flowering failure and even small breaks in the population-level flowering sequence should lead to localized loss of the species-specific pollinator population and thus to fig reproductive failure (Bronstein *et al.* 1990). Only when an unbroken flowering sequence is somehow regained will rare immigrating wasps be able to found new, persistent local populations.

In contrast to the majority of figs, however, *F. aurea* normally exhibits substantial within-tree flowering *asynchrony* (Fig. 2; see also Bronstein & Patel 1992a). Although Hurricane Andrew synchronized individual trees (and much of the population) phenologically, previous levels of within-tree asynchrony had been regained by the following spring (Fig. 2), suggesting that asynchrony is under endogenous control. This fig phenological trait appears to promote rapid recovery from flowering catastrophes. When figs become receptive to pollination asynchronously, the length of time that that tree is attractive to searching pollinators is prolonged (as is the period over which the next generation of pollen-carrying wasps departs). Furthermore, if the tree is unusually asynchronous, escaping wasps may encounter receptive figs on their natal tree itself (Bronstein & Patel 1992a), vastly increasing their usually minimal host-finding success. (*F. aurea* is self-compatible and wasps have equivalent reproductive success in selfed and outcrossed figs; M. Hossaert-McKey & J. Bronstein, unpublished data.) Hence, within-tree asynchrony can increase the likelihood that a rare wasp immigrant or local survivor will be able to found a new population, and can then allow that wasp population to persist in association with relatively few fig trees.

IMPLICATIONS FOR UNDERSTANDING FIG/POLLINATOR INTERACTIONS.—Rare events often shed light on phenomena that are difficult to study directly. The remarkable recovery of the *F. aurea–P. jimenenzi* interaction from Hurricane Andrew holds at least two implications for understanding the classic (but still poorly understood) obligate mutualism between figs and their pollinators. First, this study adds yet more circumstantial evidence that fig wasps have impressive colonizing abilities. Pollinator loss in small fig populations may commonly be only a transient phenomenon, with weaker ecological and evolutionary consequences than once conjectured (McKey 1989, Bronstein *et al.* 1990). Second, these results suggest an adaptive function for the unusual phenological traits exhibited by *F. aurea* and several other fig species (*e.g.*, Baijnath & Ramcharun 1983, 1988; Corlett 1984, Smith 1994). Ramirez (1970) and Janzen (1979) argued that within-tree flowering asynchrony would permit wasps to remain for multiple generations on their natal tree, travelling between adjacent male-phase and female-phase figs. Although resulting self-pollination might be costly for figs (but see above), it might have overriding advantages when it permits pollinator populations to survive conditions in which departing individuals would fail to find other flowering trees. Bronstein and Patel (1992a) tested and rejected this hypothesis, however, showing that asynchrony in *F. aurea* was only rarely sufficient to permit wasps to remain on their natal tree. The results presented here suggest a different advantage to within-tree flowering asynchrony: it may permit very rapid recovery from climatically induced flowering failure and the associated loss of wasps. Selection for such adaptations may be intense, given the short average return time for Caribbean hurricanes (6 years in south Florida and ranging from 6 to 21 years across the region; Simpson & Lawrence 1971, Simpson & Riehl 1981). More generally, this study has provided evidence that obligate interactions can be highly resilient to population-level catastrophes, contradicting many long-held assumptions about the costs of specialization.

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